THE WING FOLDING PATTERNS OF THE COLEOPTERA

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In working out the venation of the Coleoptera it has gradually appeared that the arrangement of the folds also was significant and would give evidence as to relationships within the order. The folding pattern was therefore studied in a series of forms, including representatives of practically all the families of beetles, and has been far more productive even than had been hoped.

The folding patterns of practically all beetles prove to be derivable by relatively simple modifications from a single fundamental plan, close approximations to which are found in various families. These modifications have taken a relatively few definite directions, each of which characterizes a large series of Coleoptera, and which in several cases I believe is as significant as any of the characters now in use. They throw considerable doubt, however, on the present placing of a good many families and genera, especially of the smaller forms.

The study is based primarily on material in the collection of Cornell University, supplemented by purchased material. I am very much indebted to Dr. E. A. Schwarz, Mr. H. S. Barber and the U. S. National Museum for the loan of many significant forms, including Cyathocerus, Hydroscapha and Discoloma; to Dr. Wm. M. Mann for the loan of Gnostus, and to Mr. A. J. Mutchler for Telegeusis and several other interesting forms.

METHODS

In the case of forms of convenient size, especially if the species were somewhat rare and I did not wish to injure the appearance of a specimen, the beetle to be studied was relaxed somewhat, which made it possible to raise the left elytron and remove the wing without visible damage to the specimen. Then a drawing was made of the venation, using a mounted specimen of the same genus when possible—in other cases a copy of any figure available, or building up a sketch from the wing being studied. Kempers' set of figures of most of the European types of Coleoptera (Ent. Mitt. 12: 71–115; 1923) was a very useful source. The position of all the folds visible in the wing was laid down on this drawing, in their proper relation to margins and visible veins. Then the outer part of the wing was partially and gradually unfolded, plotting the remaining folds as they became visible, always with reference to the veins so far as they could be seen; and noting in every case whether the folds were convex or concave as seen in the unfolded wing, and whether the areas were right side up or reversed in folding.

In some cases fresh specimens were used, and the folds studied without removing the wing, as in this way it was possible to see how many were of permanent character, and how many the result of accidents in the folding. But in general, specimens which had been dried were more useful, as the drying set the folds in, and they could be located more surely and accurately. The principal exceptions are the relatively small crumples, which proved unstable, and especially the dorsal margin of the wing, which in many forms has no definite folding pattern, but is merely packed away, apparently by use of the legs. In these cases the more obvious folds were noted in detail, and the presence of additional presumably inconstant ones is indicated in the diagrams by fine oblique hatching. Areas not completely folded over, and areas which it was not possible to work out fully, are also indicated in the same way.

With the smaller forms it was not possible to use the same method, as a relatively small amount of relaxing frequently caused the wings to unfold more or less completely, and sometimes caused the folds to vanish. In this case the left elytron was removed and the wing broken off. If the specimen was at all oily or gummy it was manipulated in alcohol (95 per cent.) which did not soften the wings enough to unfold them, but made the specimens decidedly less brittle. The wing was then manipulated as in the case of larger wings, but it was frequently unnecessary to unfold it more than a little, as the folds could be seen through several thicknesses of wing, and it was merely necessary to work out their relative position. This was usually done in alcohol, handling the wings with fine needles, but was tedious; and frequently it was not possible to work out a wing quite completely, though it was rarely difficult to determine the type of folding.

The wing was then usually transferred to weaker alcohol, allowed to unfold itself and mounted dry for the study of the venation. These small forms have lost the venation more or less completely, the outer veins being visible only in a cross light, and most of the anals often completely lost, but the foldings are by no means simplified, as will be readily seen by looking at the figures of such forms as the Nitidulidæ (the wing of *Colopterus*, fig. 51, is less than 3 mm. long). This gives the folding a very special value, as practically all the other structures, venation, tarsi, antennæ, etc., are more or less simplified in the minute species. Only at the limit of smallness (Hydroscaphidæ, Sphaeriidæ, Clambidæ, Ptiliidæ) is the folding somewhat simplified.

NOMENCLATURE

For convenience I have designated the areas delimited by the folds of the wings by capital letters, using the first part of the alphabet (A–J) for the areas reversed in folding, and the latter part (P–X) for the areas which remain upright, or which are finally upright as the result of two successive reversals. For the folds themselves I have used the letter belonging to the adjacent reversed area, combined with a number which is odd for concave and even for convex folds. These numbers and letters have been laid out on my hypothetical wing (text figure 1) and are used uniformly in all the forms where homologous folds occur.

Frequently some of the areas are subdivided by additional folds. In these cases I have added a small letter to the capital to distinguish each subdivision; new areas not obviously the product of division of typical areas are designated by small letters standing alone. These are applied arbitrarily, but so far as possible uniformly in closely related forms.

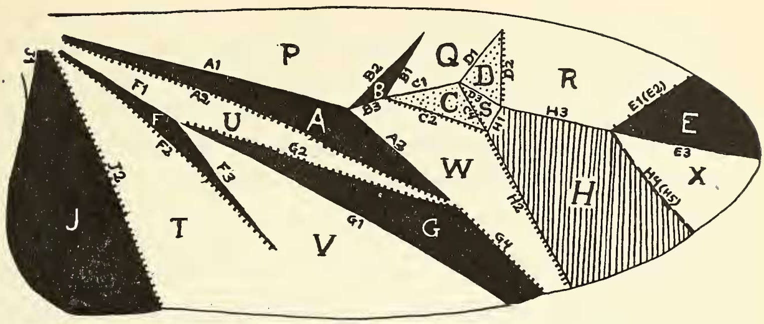

FIGURE 1. Hypothetical folding and nomenclature.

The following is a list of the principal areas (compare the figure).

A—Median	P—First	Costal
B—Proximal Pivot	Q—Second	
C—Antemedian	R—Stigmatal	
D—Pivot (Distal Pivot)	S—Central	
E—First Costo-apical	T—Wedge	When combined forming the Anal Area
F—Second Anal	U—Cubital	
G—First Anal	V—Outer Anal	
H—Principal	W—Oblong	
J—Jugal or Axillary	X—First Dorso-apical	

A few of the folds also are so fundamental in character as to deserve names.

The median is the concave fold through the wing from base to apex (A1–B1–C1–D3–H3–E3).

D1 is the concave pivot-fold.

D2 the convex pivot-fold.

H2 the principal fold.

A2 the cubital fold.

J2 the jugal or axillary fold.

Costo-apical and dorso-apical folds are named in order of appearance, the most basal being "first."

THE FUNDAMENTAL PLAN

In making up a hypothetical plan (text fig. 1) certain points must be taken into consideration. *First,* it must be derivable with only minor changes from both the Adephagous and Polyphagous types; *second,* the necessities of a practical folding must be considered. The hypothetical pattern here suggested is a slight modification of the Adephagous type, and has no element not present in some Polyphaga; and it has been tested for functional possibility by actually folding a model.

It is to be noted that folds always meet in groups of four (rarely six), save in the case of narrow crumples that fade out imperceptibly at the ends. In such a group of four, one pair always makes a continuous fold, passing through without change of character; the other pair are always one convex and one concave, and may either be placed in mirror symmetry to the first pair or may both be located on the same side of it; in the latter case the first fold always is bent at an angle corresponding to that included between the other two. The narrowest of four areas that meet at a point is always bounded by one concave and one convex fold.

Bearing this in mind we may take our hypothetical type and analyze it further, on the supposition that a fold that changes character at an intersection is later than one that passes through unchanged. On this hypothesis the folds appear to have originated in the following order:

1, the axillary fold (J2); this is present in many orders and notably in the fore wing of the Lepidoptera and Trichoptera, where it separates the jugum from the rest of the wing. No doubt the fold that separated the alula of the fore wing from the elytron proper in the Adephaga and Hydrophilidæ is also homologous.

2, the median furrow (A1–B1–C1–D3–H3–E3). This is homologous with the median furrow of Neuroptera and various other orders, and no doubt originally lay along the median vein, which was primitively a concave vein—Adolph notwithstanding. In the Coleoptera (as in the Lepidoptera and Hymenoptera) it no longer lies exactly on the vein, but alternately above and below it. If Tillyard's theory is correct, that media was originally trifid, with a convex middle branch between two concave branches, the outer part of the Coleopterous median fold (C1–E3) would have to represent the fold accompanying M_1, while C2 and H2 may perhaps represent M_2.

3, a convex fold along Cu (A2–G4).

4, a concave fold along 1st A (F1–G1).

5, a convex fold along 2d A (F2). These three folds are also more or less developed in several orders, at least as convexities and concavities along the veins. Like the median furrow they have left the veins, and in the beetles lie immediately above or below them.

The remaining folds are peculiar to the Coleoptera, except that the two hinge folds are developed toward the costa in many Hymenoptera (*e.g. Ophion*). They differ from the first set in being more or less transverse, and changing from concave to convex or vice versa, whenever they cross one of the earlier folds.

6, a zig-zag antemedial series, crossing 2, 3 and 4, and changing direction and character at each crossing (B2–A3–G2–F3).

7, the fold B3–C2–H2, crossing fold no. 1 only, and changing from concave to convex where it crosses. It is not unlikely that the convex part of this fold represents M2, and that the concave part, which is frequently absent, is a mere adjustment.

8, 9, the pivot folds, each starting from the costa before the stigma, at a point where the costal group of veins (C, Sc, R_1) are fused to form an elastic hinge; each crossing fold 1, changing direction and character, and then ending at a single point on fold 7, which changes direction somewhat as a result. These folds are absent in the Liodes group, and a few others, but probably not as a primitive character. Their costal portion is present in the Hymenoptera.

10, a subapical fold, not constantly present; and not constant in character, normally being concave at the costa in the Adephaga, and convex at the costa in most of the Polyphaga which have it.

THE INDIVIDUAL AREAS

The hypothetical type, as just constructed, is not found exactly in any form known to me, as none of the Serricornia, Clavicornia, etc., which have a typical preanal region, show the two adjustment folds in the anal region. Following are the principal modifications of the various areas.

A. The median area lies between media and cubitus in the basal part of the wing, terminating when well developed in a point which rests on cubitus at the angle of the first anal area.

Among the Adephaga A is typical in the Hygrobiidæ, Haliplidæ, Bidessus and the Rhysodidæ. More frequently it is broken up at the middle to make an adjustment with C + D. In the Cicindelidæ and Carabidæ the adjustment usually takes the form of a small triangle which is folded back, interrupting the area opposite the apex of C, as shown in the figures of Cincindela and Calosoma (figs. 6 and 7). In the Cupedidæ and Paussidæ there is quite a different arrangement, an additional reversed area (a) being interpolated along the course of the median fold, and separated from the surrounding areas (Aa, Ab, C + D) by two adjustment triangles. In the Geadephaga the oblong cell does not reach Cu, and the tip of area A reaches nearly or quite to H; in the Hydradephaga there is a well-developed first anal area which intervenes. Paussus and Nebria are intermediate, having a well-developed first anal area, and a small oblong cell resting solidly on Cu (fig. 10). Paussus is in every other way close to Brachinus, and Nebria has always been reckoned with the Geadephaga.

In the remaining Coleoptera area A is of subordinate importance, and is never divided. Frequently it is reduced to a mere crumple (as in most Serricornia), or even absent (Cucujus). In quite a list of forms it is reversed, the convex fold coming above the concave. Examples are: Dermestes, Trogosita, Helota, the Phytophaga so far as examined, and those Bostrychoids which have the area well developed. In the Sternoxia and Erotylidæ, including Phalacrus, it appears to be normal or reduced to an amorphous crumple, and also in most forms with the Staphylinoid folding. In the Dermestid genus Megatoma it is divided into two as in the Adephaga, but has its convex over its concave fold as in other Bostrychoids. Among the Dryopoids it is reversed in the Mycetophagidæ.

B is rarely well developed and may perhaps be of secondary character. It is absent in the Adephaga, and in a very large proportion of forms (including all the Heteromera examined) is a minute crumple which can hardly be represented in a diagram. In many forms with a short median recurrent vein it becomes an important part of the folding mechanism, especially in the more typical Bostrychoids, where it functionally takes the place of area A, and works with the anal fold in a similar way (figs. 69–76). In the immediate Dascyllis group, as also in Sphindus and Corticaria, there is an imperfect area at this point, but with the concave fold before the convex one. Presumably this is really not B, but a semi-independent part of C. B is best developed in Artematopus and Macropogon, where it works with area A, and ends at a notch in the median vein, and in Anthrenus, Cyphon, and the Ptinids and Bostrychids, where it works with the first anal area. In the aberrant Dermestid genus Megatoma, Nosodendron, Sphindus, and Corticaria it crosses the end of a short median recurrent, but terminates at area A. In those Dryopoids and forms related to the Coccinellidæ where it is present it is of the Dascillus character, and in some can be changed from a considerable area to a mere crumple, by a slight change of the position of the wing. The Melyridæ and some Byrrhidæ are the only decided exceptions I have seen, and perhaps belong to a different stock from the rest.

C is an important fold. In practically all Polyphaga it is well defined, but varies enormously in size, even in closely related genera. Thus in Hydrous it practically reaches the base of the wing, while in Hydrocharis and Helophorus it is short. In the Elateridæ and Lampyridæ it is very long, while in the closely related Lichadidæ and Buprestidæ it is short. It is long in Cucujus and Passandra, but short in most other Cucujidæ; long in Litargus, but shorter in Mycetophagus. Where it works with a well-developed area B it is always short. Frequently it fuses more or less completely with the neighboring areas—with B in the Dascillus group and Dryopoids, with D in the Adephaga and with both D and H in the higher Melyridæ. In many Staphyliniformia where the base of the wing is reduced, area C is very narrow, though fully functional, but it vanishes completely in such forms as the Liodidæ and Octhebius.

In a few forms, all Bostrychoids, C is divided in two by a triangular area which works with B. Examples are Corticaria, the South American Bostrychid figured, and apparently Dascillus.

This gives a close resemblance to forms in which D is reduced, with its apex resting on the inner side of E, but may be distinguished by the fact that the transverse fold at the end of the cell is concave instead of convex.

E. The first costoapical area begins to show the relative instability characteristic of the whole apical region. The costoapical region presumably was undivided in the original Coleopter, as its dividing fold is concave in the Adephaga, including Cupes, but convex in practically all the other Coleoptera. Where it is absent, however, I suspect a secondary loss. Examples are the typical Bostrychidæ, and Dascillus, though in the presumably more primitive Cyphonid and Sphindid types it is present. It is also absent in Dermestes, and is of the Adephagous type in some Buprestidæ and Phytophaga, Megatoma and Attagenus, where it presumably is secondary. In the Adephaga it is invariably present and typical in character, making one leaf of the double apical roll in the Archostemata.

Other apical folds are so complex and variable when present that they had better be discussed under the individual families. They are evidently secondary in character, and due to an enlargement of the apical part of the wing, except in the few Adephaga where they are symmetrically placed to the median furrow and may be the result of flattening out of the apical roll (Bidessus, Hygrobia, Haliplidæ, Rhysodidæ, Cyathoceridæ, Sphærius). The most complex apical foldings I have yet seen are in the Nitidulidæ (figs. 51–53) and Cryptophagidæ (fig. 137).

Anal folds. When fold A is well developed and terminates before the end of the cell, or when B is well developed and A is absent, a fold below Cu is needed to allow Cu to bend. This is the first anal fold (G). It in turn needs a smaller adjustment fold at its proximal end in many cases (F). In the diagrams these two folds are only shown when well characterized. In many other forms one or both are indicated by slight crumplings of the wing-membrane, which may even appear only when the wing is partly unfolded. Their disappearance is so gradual that F is of no use in classification, and G only in a certain proportion of cases.

In the Hydradephaga, in connection with the large size of the oblong cell and the shortness of A, G is always well developed, in the Geadephaga and Rhysodidæ it is usually represented by a slight crumple only; but this narrow crumple frequently functions in exactly the same way as the large area of the Hydradephaga, so that the difference is one of degree, and not of kind. The Paussidæ show an intermediate state, that is undoubtedly ancestral.

In the Polyphaga A is rarely sufficiently strong to require adjustment at its tip, and when it is, it usually reaches the tip of the cell, working with area H. Usually it is area B which makes a strong adjustment system necessary. Examples are principally from the Bostrychoidea (Megatoma, Nosodendron, the Helodes group, Anthrenus and the true Bostrychidæ). In Nosodendron A is well developed and short as in the Adephaga, it also appears among the Dryopoids in the curious Ptilodactyla group, where it is an adjustment not so much to A or B as to H, which crosses the tip of Cu, and necessitates some complicated folding in the anal region. In most Haplogastra it has developed differently, as a slender longitudinal fold crossing the basal side of H at right angles, and evidently serves not as an adjustment to other folds, but as a means of further narrowing the wing. In the Scarabaeoids this area is always striking; in many others it tends to disappear, but is shown, for instance, in Cercyon, Georyssus, Sphaerites and Syntelia, Sericoderus, Monotoma and the Cryptophagidæ. In several, perhaps most, others it is indicated by a slight crumpling of the wing. In the Serricorns and Clavicorns it is also a slight crumple which is frequently absent, and does not cross into area A.

H is an area comparable in importance to C and D. Typically it lies between the median fold and C, and extends about half way to the apex of the wing, being cut off by the same transverse fold that cuts off the first costo-apical at the base. In the whole large group of Haplogastra it is increased by the addition of a reversed area below Cu, formed apparently in the first case by a convex fold from the tip of the cell to near the tip of 2d A_1, and a concave one along the lower side of Cu. This concave fold and the convex one just above Cu tend to neutralize each other, and functionally at least the whole of H is a single area; in several forms in fact the two folds along Cu have completely disappeared, and the area is undivided (fig. 53).

In those forms where E has disappeared, area X is also absent and H reaches the apex of the wing. In a similar way, when the anterior side of E creeps forward on the costa to the end of the cell, the posterior side of H tends also to creep forward, though not always symmetrically. The first stage of the process shows in such forms as Hydrocharis (fig. 25), while it reaches the extreme in the Derodontidæ and Coccinellidæ on the one hand, and the Micropeplidæ on the other.

In a group of forms of the Dryopid type of folding this migration is carried to an extreme, and area H is reduced to a small quadrangle near the middle of the wing, either barely touching the inner margin or completely separated from it. This is strikingly shown in the Derodontidæ, already mentioned, and in the series of families grouped around the Cisidæ. In most of these forms Cu is disturbed, turning directly to the inner margin to avoid the transverse fold in the Coccinellidæ and Collops; but cut off by it in Derodontus and Malachius. In the Byrrhidæ and genera related to Ptilodactyla this fold can be seen gradually working up from the apex of Cu more than half way to the point of anastomosis of Cu and M_4. In the Cryptophagidæ, on the other hand, it is not at all clear what has happened, though they appear on the whole to belong to this series. At first glance the Nitidulidæ seem similar, but the folding is much closer to that of the Brathinidæ and Staphylinidæ. Their venation is also approximately as in the Synteliidæ.

Another modification is the subdivision of area H. This in a definite way is practically confined to the suborder Adephaga, where a series of alternately convex and concave longitudinal folds may divide the area into as many as five separate portions, each corresponding to a slip in the apex of the wing.

In those few primitive Adephaga where C and D are still separated by a trace of the median fold (*e.g.*, Paussus, figs. 11, 12) the median furrow seems to attach to the second, rather than the first of these slips, the first being perhaps a development special to the Adephaga.

The area below G, which is added to H in the Haplogastra, is also apt to be complexly folded according to a plan which varies from family to family. Finally it is the habit of many beetles to tuck in the hind edge of the wing by main force, resulting in a system of minute and irregular folds along the inner margin. These have usually been omitted from the diagrams.

Subapical area. The dorsal portion of the subapical area is even more unstable than the costal portion, though it shows resemblances in closely related forms; and the few points of interest will be discussed under the individual families.

The axillary region (J), corresponding to the jugum of the Lepidoptera, varies mainly in size. Primitively it is a broad sessile area, as in the more primitive members of all the groups. In a considerable variety of families and lesser groups it is a free lobe, and in stray types it is completely lost, the most striking cases being the Liodidæ with their kin, and the groups centering around the Cisidæ and Hydroscaphidæ. The identity of Cisidæ and Corylophidæ is specially striking. In the family Colydiidæ, as now delimited, every degree of development of the anal lobe is found. In the little Hydroscaphid group the entire anal region is obsolete.

The unreversed areas as a whole have little individuality or interest, appearing to be merely the portions of the wing left over. S alone, which is really twice reversed, rather than unreversed, alone shows some positive characters. Its usual form is a triangle with concave upper and outer, and convex lower side, adjoining areas D, H and C. In a few forms it is complex, made up of three or more areas. This may possibly be a primitive condition, as it occurs in such early families as the Elateridæ and Hydrophilidæ, as well as some Lamellicornia (Lachnosterna). In the Buprestidæ only a single one of these areas seems to have survived, but not the same one as that of most other families. It is distinguished from the usual area S by being reversed, with convex upper and outer sides, and concave inner, and its apex lies much farther out, on the fused part of M and Cu, and not as usual on the free part of M. I am distinguishing it by a small s. In more specialized Buprestidæ, and in a scattering of other forms, S vanishes, usually where areas C and D have become of subordinate importance. In the Staphylinidæ, Histeridæ and Nitidulidæ, however, though reduced, it takes its normal part in the folding of the wing. A few of the primitive Adephaga show faint traces of it, crossing the area C + D, but as a rule it has disappeared.

CLASSIFICATION

In the following discussion of the characters of the various groups a classification has been adopted based primarily on the wings. I by no means believe that it is the last word, but do think that in some particulars new light has been thrown on the relationships of the families. It is noticeable that most of the types moved to new localities are forms already of disputed position, and that a specially large proportion belong to the old group Clavicornia. In several cases results obtained from the study of the venation without considering its relation to the folding have had to be abandoned; the Staphyliniformia, in particular, which Continental entomologists have consistently defined on venational characters, is reduced to a subordinate position, and several forms with much reduced venation have had to be added to or subtracted from it. The other most striking change is the discovery that in various families two entirely different types of folding occur, which are not really even derivable from each other. The most striking case is the series of families in which Dascilloid foldings and Dryopoid foldings occur and the intermediate Serricorn-Clavicorn type is absent. These are: Byrrhidæ-Nosodendridæ, Helodidæ-Eubria, Dascillidæ-Ptilodactyla, Lathridiidæ-Corticaria. In other cases there is the possibility of derivation, but it seems unlikely. For instance the group associated with the Liodidæ seems entirely homogeneous, but on superficial characters associates itself with the Hydrophilidæ, Silphidæ, Staphylinidæ and Brathinidæ, and there is nothing to prove from which of the four it has been derived; in fact even some Dryopoidea show a closely similar type of folding. This convergence is the most difficult point in the entire scheme, as the final product of specialization of the Hydrophilid and Dryopoid types would come to the same point.

The Adephaga are adequately defined on the type of folding. The Archostemata resemble them, and seem to be separated by the spiral rolling of the apex. The remainder will separate into four groups according to the direction of specialization.

1. In the group of which the Hydrophilidæ are typical, the tip of M_4 is folded across. In primitive members at least, Cu is not fused with M_4, and may avoid the fold, in the higher ones it is not clear whether Cu has fused with M_4 or atrophied. This folding is accomplished in the first place by the crumpling of the dorsal region between Cu and 2d A, as well shown in the Histeridæ, as well as some Hydrophilidæ; only later is this area joined to the normal area H, and M_4 actually reversed, M_4 more typically pivoting back on its base; but the unreversed area which contains it is very narrow, and the folds are so close to the vein that it is frequently impossible to tell if the vein itself is reversed or not. The first costo-apical fold in this series is much slower to migrate toward the base, and the stigma remains for a long time as a well-marked chitinized area beyond the hinge, which is stiffened by a chitinized vein, and in the larger Staphyliniformia even shows two veins in close contact. Several forms of this series have retained the anal arculus (Necrophilus most conspicuously), and other signs of primitive position are the frequent presence of the pleurite of the second segment of the abdomen (Hydrophilidæ as well as the families included by Kolbe in his Haplogastra), and the frequent membranous alula of the elytron (never present in the remaining groups). This group would better deserve the name of Clavicornia than the group which carries it, as clavate antennae are far more nearly universal than in either of the other groups. The main group of anals is invariably reduced.

2. The group of which the Elateridæ are typical represent most closely the primitive type of folding, as the pivot fold is well marked, and not associated with any other fold, and M_4 and Cu (which are invariably fused) are not crossed by a fold. This group on other characters shows less primitiveness. The stigma is never distinct, though in a few primitive types the chitinized costa passes a very short distance beyond the hinge; the anal arculus is never present; the second pleurite is visible only in very loosely built degenerate forms, and the alula of the elytron is never present.

The two following groups are undoubtedly derived from this one. In the case of the Bostrychiformia survivals of an intermediate condition are found in the Dermestidæ and Buprestidæ, while the Lichadidæ, which otherwise are very close to the Rhipiceridæ, belong clearly to this group on folding, and must more closely than any other living form represent the common ancestor. Zenoa is our native representative. It is not possible to pick out definitely the immediate ancestor of the fourth series, if indeed it is homogeneous, but many forms of this series show a tendency for the first costo-apical fold to migrate toward the hinge. The ancestor must have been an early form in which the hinge was still chitinized, and traces of the stigma present, as these are clearly recognizable in some of the Dryopoid group. The most plausible link is perhaps from the Lichadidæ to Dæmon.

3. The Bostrychoids are adequately defined by the fact that the hinge is broken up by the migration of the convex hinge-fold toward the apex. This could not have taken place in a type where the hinge was still chitinized; but in other characters this group shows signs of extreme primitiveness. All the forms which have preserved a distinct frontal ocellus (except the Cupedidæ and a few Lymexylidæ) belong to this group; and this group, especially the forms transitional to the preceding, show more free anal veins than any others except a few Lampyridæ. The preservation of 4th A_2 in a few forms is unique in the Polyphaga. The type seems made up of a mess of relicts, and the families are hard to delimit, such a family as the Dermestidæ, for instance, being the real equivalent of five or more ordinary families. There is never any tendency for $M_4 + Cu$ to be disturbed, and anal arculus, alula and visible second pleurite are never present.

4. The Dryopoid complex is defined by the fact that the first costo-apical fold has moved basally and joined with the hinge, so that three folds converge at a single point on the costa, and the outer part of the wing is folded directly back on the base. In the true Cryptophagidæ even a fourth fold has converged on this point. There is a strong tendency for the principal fold and first dorso-apical also to migrate toward the base of the wing, and in the more specialized families there is a close likeness to the more specialized Haplogastra; in fact I am uncer-

tain to which series such families as the Georyssidæ and Mycetaeidæ belong. The type is easily derived from the second by the migration of a single fold, and may not be homogeneous, though there seems to be a distinct linking of the various families, especially through the Colydiidæ, which in genitalia also, according to Sharp and Muir, form a link between several principal types. Superficially the closest resemblances are to the preceding type, from which this hardly can be derived. I know of no special primitive character in any member of this group except the apparent trace of the anal arculus in some Coccinellidæ.

The diagrams hereto attached may make plainer the appearance of the principal types of folding as they look in the undisturbed wing.

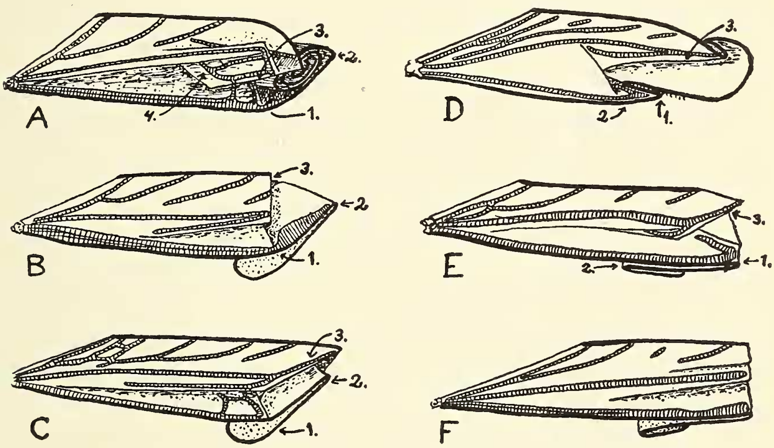

FIGURE 2. Folding patterns as shown with wings folded. A, Adephaga; B, Haplogastra; C, Diversicornia; D. Bostrychiformia; E, Dryopiformia; F. Ambiguous.

These diagrams represent a left wing seen from in front and above. The margins are represented by thick lines, so far as visible, the folds by fine lines, and the veins by double lines with cross-bars. The apex is represented as if drawn forward somewhat, to show the subapical fold, which would be covered by the basal part of the wing in the completely folded position.

Adephaga (Diagram A). 1, costal edge turned back at pivot; 2, apex of costa folded up and over; 3, principal fold cutting off Cu (not in Archostemata); 4, oblong area tucked under Cu (not in minute forms).

Polyphaga, Series 1 (Diagram B). 1, costal edge turned back at pivot; 2, apex of costa folded down and under; 3, principal fold cutting across M_4 (and Cu) at base.

Series 2 (Diagram C). 1, costal edge turned back at pivot; 2, apex of costa folded down and under; 3, principal fold running beyond $Cu + M_4$.

Series 3 (Diagram D). 1, costal edge folded *up and over* at pivot; 2, then folded out again beyond; 3, principal fold running beyond Cu.

Series 4 (Diagram E). 1, costal edge folded *down and under* at pivot (the true pivot-fold obscure); 2, and then out again near apex; 3, principal fold avoiding $Cu + M_4$, or crossing it beyond its base.

Ambiguous type (series 1 or 4) (Diagram F). Pivot obscured, a transverse convex fold right across the wing, which is also once longitudinally plaited. Apex folded at least once more.

ADEPHAGA

C fused with D more or less completely, never separated by a definite re-reversed area, apex of C + D resting on M or crossing it and working with a large area A, which invariably has its upper fold concave, *B always absent; first costo-apical fold concave; following ones when present usually also concave; principal fold crossing base of M_4*, and cutting off Cu at its base; median fold always interrupted at the hinge, but *wing with a complete transverse convex fold. Costa chitinized at hinge,* frequently showing two veins; *stigma conspicuous;* Rs connected to stem of R, two radiomedial cross-veins; oblong cell almost always present (also in Sphaerius); at most four anals in principal group; 4th A normally forked, the forks gradually divergent; anal arculus well developed. The characters italicized apply also to the minute forms of the Hydroscaphid group.

GEADEPHAGA

Oblong cell small, usually connected to Cu by a short piece of simple transverse vein (except Nebria and Paussidæ); only one concave costo-apical fold, the folding of the apical part of the wing dominantly longitudinal; first anal fold a mere crumple.

Cicindelidæ: Median fold continuous from lower angle of hinge area to apex; oblong cell absent (figs. 5, 6). Tetracha agrees with Cicindela, but Pogonostoma, which has preserved the oblong cell, was not studied. Apterous forms are well-known.

Carabidæ (figs. 7–9): Median fold from lower angle of hinge area ending at the costo-apical fold, the median fold of the apical part of the wing abutting against the outer side of the oblong area. Oblong cell present with rare exceptions, and (I believe) always indicated by an irregularity of m–cu. Hinge area usually simple, broken up in Brachinus, which approaches the Paussidæ; first anal area negligible. Adjustment between areas A and C + D made by a single re-reversed fold. There are many apterous forms.

Omophron: Entirely typical of the Carabidæ.

Nebria: Folding entirely typical, but oblong cell resting on Cu, and first anal area perhaps a little better developed than usual. Elaphrus and the other related genera are normal.

Brachinus (figs. 8, 9): Adjustment of C + D and A nearly normal, but a little irregular; C + D crossed by a well-marked median furrow, and region immediately beyond with a set of four extra folds, as in the Paussidæ. First anal area normal.

Paussidæ (figs. 10–12): Oblong cell very small, but resting solidly on Cu, and anal area much larger than normal in the Carabidæ, though smaller than in the Hydradephaga. Folding at hinge region highly complex, with area C + D divided, and several small folds beyond it. C adjusted to A as in the Cupedidæ. Median fold in apical portion divided in two parts as in Carabidæ. M_4 arising from lower corner of oblong cell, instead of from its upper portion.

HYDRADEPHAGA

Oblong cell very large (figs. 13–17), with a large first anal area below it and a well-marked second anal area working with the apex of the first. There are two thoroughly distinct subtypes in this group, which will divide in the midst of the family Dytiscidæ; in the Hygrobiidæ (figs. 14, 15), Haliplidæ (fig. 16) and Bidessus (fig. 17) group there is a succession of concave costo-apical folds, no doubt produced by the flattening out of a spiral roll such as that in Cupes; area C + D touches area A at a point, without any adjustment fold, and the first anal vein is strongly curved, without any accompanying chitinization.

In the remaining Dystiscidæ (both Fragmentati and Complicati) as well as the Amphizoidæ and Gyrinidæ (fig. 13) there is only one costo-apical fold, corresponding to that of the Carabidæ, C + D joins area A broadly, producing a re-reversed adjustment area, and 1st A is straight and normally accompanied by a strong chitinization of the membrane. (See Forbes, '22, fig. 18.)

The following four families have universally been scattered among the Polyphaga, but the first of them shows unmistakable characters of the Hydradephaga, both in wing and other body characters, and the remainder show at least some traces of Adephagous characters and are linked to them. With Clambus these Adephagous traces become negligibly small, and the genus was viewed by me as of hopelessly uncertain affinity until I examined the linking types.

As a group they are characterized by the relations of area C + D, which is large and nearly equilaterally triangular, and extends the whole distance from R to Cu, vein M being absent or reduced to a short stub, and area A obsolete. The anal region is reduced, and is of substantial size only in Cyathocerus, where area G is also normal.

CYATHOCERIDAE

Cyathocerus horni (figs. 19, 20). Veins well marked, oblong cell longitudinal in the wing (an exaggeration of the Haliplid character), without any trace of the tip of Cu; three successive concave costo-apical folds (leaving out of account a small crumple), and three convex dorsoapicals. Anal region but little reduced, with large area G and well-marked F, anal lobe functional, and a second notch in margin at apex of 3d A_1, as in the Haliplidæ. Elytron deeply toothed at the costal edge, an exaggeration of the tooth present in the Haliplidæ, but apparently adjusting to the legs, rather than forming a lock with the body.

First visible ventral segment divided into a small central and lateral portions as in Adephaga; but mouth-parts reduced, not Adephagan-like, and first tergopleural suture not visible.

SPHAERIIDAE

Sphaerius acaroides (fig. 21). Wing with anal region lost, carrying with it areas F, G and J, the large area C + D practically reaching the inner margin. Veins weak, but costal group and Cu functional, and with a spring-like structure which closes the wing when relaxed as in other Adephaga. Oblong cell fully traceable, but very weakly chitinized. Apex of wing with two convex dorsoapical and two concave costoapical folds, besides some confused ones. Fringe long and heavy, rather Ptiliid-like in the folded wing, but relatively shorter. Body structures reduced, with nothing definitely Adephagous; but habits apparently Haliplid-like.

HYDROSCAPHIDAE

Hydroscapha sp. (fig. 22). Wing as in the Sphaeriidæ, but with venation more reduced and oblong cell lost. Body superficially Staphylinid-like, with fully chitinized second abdominal segment; tergopleural suture apparently preserved (the specimen before me is broken evenly and symmetrically on that line).

CLAMBIDAE

Calyptomeris alpestris (fig. 23). Wing much more slender than in the preceding forms. Area H working directly with the apex of C + D, without the intervention of a portion of E or secondary crumples, and bounded on the outer side by a concave, instead of the usual convex fold. Fringe subordinate in character.

Clambus armadillus (fig. 24). Wing even longer, the outer part crossed by a pair of transverse folds, Cu lost as a functional vein, and area C + D crossing its site and resting broadly on the inner margin (a unique character).

In the Clambidæ the only truly Adephagous characters surviving are the presence of one or two concave costo-apical folds, and in Calyptomeris the presence of a convex fold clear across the wing from the pivot to the inner margin, while the concave median fold is much interrupted. In other parts the only possible Adaphagous character is in the ædœagus, which has a partly free tongue on the ventral face as in many Hydradephaga.

RHYSODIDAE

Oblong area absent (fig. 18), as in Cicindelidæ, m–cu being straight; hinge area touching A at a point, without any adjustment area; apex with a series of concave costo-apical and convex dorso-apical folds as in the Hygrobiidæ and Peltodytes; first anal area obsolete. Anal venation characteristic and stigma nearly filled with a chitinization.

Clinidium is apterous; and the group of Colydiidæ formerly associated most closely with the Rhysodidæ are also apterous.

ARCHOSTEMATA

General type of folding as in the Adephaga; apical part of wing coiled in a double conical roll, the costal part concave and dorsal part convex; principal fold not crossing Cu, which practically reaches the margin, and has a well developed anal fold entirely below it. C + D adjusted to A through a group of four folds, one of them reversed, with its concave side facing M and continuous with the concave upper sides of the hinge and median areas. Oblong cell large, and first anal area correspondingly large, working with the tip of the median area. Stigmatal cell large, conspicuous, upright; two complete radiomedial cross-veins, with a broken one between them; five anal veins sometimes present in principal group, and 4th A forked, with its posterior branch running directly across to the inner margin.

This characterization will fully apply only to Cupes (figs. 2, 3) and Priacma, the other forms differing by more or less drastic reduction; though I think the spirally rolled apex and adephagous type of hinge are common to all. The isolated position of the group has generally been recognized. The peculiar type of forking of 4th A reappears in the few Polyphaga that have preserved it (Dascillus, Sandalus, Cyphon), and somewhat surprisingly in a few early Hymenoptera.

Cupes (figs. 2, 3): Venation fairly complete, about a third of the wing formed by the spiral roll.

Micromalthus (fig. 4): Venation much reduced, and basal part of the wing also reduced in area, half of the whole wing being taken up by the spiral roll. Micromalthus has nothing to do with the Lymexylidæ in venation or folding, the Lymexylidæ being normal Serricornia in those particulars.

POLYPHAGA

Pivot fold almost invariably divided in two by the interposition of a triangular unreversed area, rarely reaching the median vein, and in that case rarely working with a large and normal area A (Dryops is the most striking case). Median fold almost invariably continuous from near middle of wing to apex, the principal transverse fold not continuous to the costa. Costo-apical fold when present almost always convex; principal fold crossing M_4 in a minority of forms only (Haplogastra and weevils). Costa frequently not chitinized beyond hinge; stigma always more or less indefinite, and more often than not completely lost; first radiomedial cross-vein rudimentary in a few early forms (*e.g.*, Dascillus), usually absent; second, complete (the one that is broken in Cupes and absent in the Adephaga); third reduced to a vague thickening or absent. Rs only exceptionally connected to radial stem directly, though often by a cross-vein which may swing into the position of the lost connection in forms which have a small radial cell; oblong cell never present as such, in one or two forms with a faint trace of the first medio-cubital cross-vein far toward the base of the wing; five or even six anals frequently preserved in the principal group (1st A, 2d A, 3d A); 4th A simple save in a very few Bostrychiformia (Dascillus, Sandalus and Cyphon, and traces in a few others), where it forks as in the Archostemata. Anal arculus preserved only in a few primitive forms (Staphyliniformia, Coccinellidæ).

As already announced, this suborder, which is the largest and most varied of the Coleoptera, divides naturally into four folding types. The first, which I shall call Haplogastra, as it closely approximates Kolbe's group of that name, has the largest number of characters of the Adephaga, and should be undoubtedly considered the most primitive; and the Dryopoid is certainly the most specialized. In its folding the "Normal" group is more primitive than the Bostrychiformia, as well as in the occasional preservation of traces of the chitinized hinge and stigma, but in other characters certain Bostrychiformia have a surprising number of archaic characters, and the two groups undoubtedly separated at an early date; their intergrading is due to the survival of such known highly archaic types as the Buprestidæ, and such synthetic forms as some Dermestidæ and the Lichadidæ.

HAPLOGASTRA

Principal fold crossing M_4, and frequently Cu also; M_4 and Cu sometimes being separate; commonly ending near the tip of 2d A_1; costal chitinization at hinge usually distinct, stigma more or less obvious, though never as sharply defined as in the Adephaga and Archostemata (absent in the highly aberrant Nitidulidæ, Rhizophagidæ and Monotomidæ); the first costo-apical fold as a result never quite meeting the hinge. Apical venation frequently preserved more or less completely, most completely in the larger Hydrophilidæ, but traceable also in many Staphyliniformia, Lamellicornia and Histeridæ. Never more than four anals in principal group. Elytron frequently with membranous alula; second pleurite present as a small triangular sclerite covered by the elytron (frequently lost, but I believe by atrophy, not by fusion as in other groups). Recurrents more or less reduced in most forms, the radial recurrent reaching basad of the cross-vein only in the Hydrophilidæ, and even the median recurrent being lost in the Staphyliniformia, though preserved at least as far back as the cross-vein in the Histeroidea.

I make four superfamilies of this series, though they are not quite sharply separated. The Palpicornia include only the Hydrophilidæ, with the Georyssidæ as a doubtful appendage, and even of the commonly accepted Hydrophilidæ, Octhebius and Hydraena are to be excluded, as closely related to forms universally accepted as Staphyliniformia. The Staphyliniformia include those that have lost the whole mechanism of the recurrent veins, including the radio-medial cross-vein, and tend strongly to reduce the hinge mechanism. They, however, have preserved the anal arculus in the larger species, and are highly primitive in body-structure. They subdivide into two groups;—in the forms centering about the genus Silpha the hinge, though small, is fully functional, and the outer part of the wing is bent back at that point about 60° as if by a hinge; in those centering about Necrophilus this mechanism is lost, and the outer part of the wing is doubled directly back by a transverse fold, homologous with that in the Dryopoidea. They differ from the Dryopoidea, however, in the dorsal transverse fold (principal fold) cutting across M4 + Cu practically at its base. The third group centers about the Histeridæ, which are characterized by the very heavy loop formed by the recurrents and r–m, though the radial recurrent at least does not pass basad of r–m. Three of the families (Histeridæ, Sphaeritidæ, Synteliidæ) are closely bound together, and have preserved a well-marked hinge-thickening and stigma. In the Nitidulidæ, Rhizophagidæ, and Monotomidæ the costal thickening stops at the hinge, but the presence of the recurrents excludes the families from the Staphyliniformia, which their folding most closely resembles, and they may be attached tentatively to Sphaerites. Lameere has already noticed the likeness between Sphaerites and the Nitidulidæ. The Synteliidæ make a definite link in folding and venation as in other characters between the Histeridæ and the Lamellicornia, which form the fourth group. In the latter the first costo-apical fold never runs obliquely in toward the base as in the Hydrophilidæ and most Nitidulidæ, but is normally transverse when present; the radial recurrent and radial cell are reduced to a hook, which rarely shows any membrane in the center; the cross-vein is completely lost, but the median recurrent is long and well-developed. The apical venation does not form a regular pattern as in the Hydrophilidæ, but is represented by a great number of fine striations—a character also present in Histeridæ. There is nothing in the wing to give this group its isolated position, in fact so far as wing is concerned the Histeridæ and their kin might well be transferred to the Lamellicornia.

PALPICORNIA

Hydrophilidæ (figs. 25–28). Both recurrents and cross-vein r–m present, the medial recurrent sometimes running nearly to the base. Cu free from M_4, but sometimes reduced to a spur (Sphaeridium). Area C well developed, in Hydrous (but no other genera examined, not even Tropisternus) extending far to the base of the wing, as in the Serricornia. First costo-apical fold strongly oblique down and out from the costa, the first posterior typically symmetrical with it, but not intersecting with the principal fold as a rule, and never dividing area H into two well-marked separate areas as in the Staphyliniformia. Octhebius and Hydraena (doubtless all the genera with more than six abdominal segments) do not belong here, but with the aberrant "Silphidæ."

Hydrous: Median recurrent and area C extending almost to base of wing. Anal lobe sessile (also in Hydrocharis).

Cercyonini (figs. 26, 27): Cu reduced to a spur; anal lobe free, or of odd shape.

Helophorini (fig. 28): Apical area enlarged and complexly folded; anal lobe free. H divided in two.

Georyssidæ (fig. 49). A family of uncertain position. Sharp and Muir report the genitalia similar to those of the Hydrophilidæ, and the wing is as easily placed here as anywhere. Pivot chitinized, connecting to a short but heavily chitinized stigma which rests on the costa, unlike those few of the Liodid-like and Dryopoid groups in which the stigma is perceptible. Rr lost and Mr not really extending back of the position of the cross-vein, which is well-marked. H divided in two parts, as in many Staphyliniformia and Dryopoids; the lower one crossing the position of the apex of M4 + Cu, which, however, is obsolete. Hinge fold a mere crumple, sometimes lost. Anal lobe slender but sessile, much as in Cercyon. Apex unfolded, as in the Coccinellidæ.

The folding has gone so far in specialization as to be ambiguous between the Hydrophiloids and Dryopiformia. In the former the well-marked Mr throws it out of the Staphyliniformia which it otherwise approaches; and the strongly chitinized hinge and peculiar anal lobe suggest the Hydrophilidæ, where the genitalia would place it. The inwardly oblique position of the first costo-apical fold is also Hydrophilid. There is no resemblance in the wing either to the Dryopidæ or to the Cyathoceridæ.

STAPHYLINIFORMIA

Recurrents both lost, and r–m also lost. Hinge fold and area C relatively small or absent. Area H consistently divided in two, the upper part reduced to a small triangle or quadrangle in the center of the wing; area D when present with some tendency to be drawn out in a long triangle pointing toward the apex of the wing, as in the Nitidulid type; first costo-apical fold not oblique.

A

Hinge functional, the apex of the wing being turned back at an angle of about 60°; first costo-apical fold well beyond it, leaving a large oblique stigmatal area.

Silphidæ (Forbes, '22; fig. 25). Silpha, Necrodes, and Necrophorus, with a couple of exotic genera, alone seem to make up this group.

Staphylinidæ (figs. 31–33). A heterogeneous mass, with a highly varied folding pattern. In Anthobium the median fold follows close above the median "Strahlader," as in the Nitidulidæ, and the pattern is otherwise similar, but the loss of the recurrents makes it an impossible ancestor of the Nitidulidæ. *Micropeplus* does not belong here.

Scaphidiidæ (fig. 30). The relatively simple folding indicates an early type. *Scaphisoma* is similar to Scaphidium, but has lost the anal lobe more completely.

Brathinus (fig. 29), like the Scaphidiidæ, has an early type of folding, and shows no resemblance to the more normal Scydmaenidæ.

B

Area D absent, its position indicated in large forms by a faint oblique line, with a trace of the stigmatal chitinization below it; C completely fused with H, together making a small triangle in the center of the wing, which is cut off by a transverse fold clear across the wing.

Dr. Böving informs me that in larval characters this group is diphylectic; the Liodidæ having a larval type quite distinct from that of the Scydmaenidæ and Pselaphidæ, though both appear as nearly Staphyliniform as anything. It would appear that the Liodidæ are descended from something like the ancestor of the Hydrophilidæ and Staphyliniformia, while the others are nearer to some of the more aberrant Staphylinidæ. The larva of Micropeplus is unknown, so it remains ambiguous, but presumably goes with the Pselaphidæ. The Georyssidæ have a close approximation to the folding of this group, but the entirely different stigma and well preserved Mr and r–m make direct connection impossible.

Liodidæ (including Necrophilus and Prionochaeta), *Octhebius, Hydraena* (figs. 34, 35). Outer part of wing divided twice longitudinally and once transversely. Anal lobe free (Necrophilus, Forbes, '22; fig. 27), or obsolete.

(*To be continued*)